"NORMAL" EXTINCTIONS OF ISOLATED POPULATIONS

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INTRODUCTION

Case studies of extinction fall along a continuum with respect to suddenness, extent, and identifiable causes of extinction. At one extreme, the dramatic end of the spectrum, are extinctions or extinction waves due to some clearly identifiable event. Some of these dramatic extinctions were sudden, in the cases of events that were themselves sudden rather than gradual. Some consisted of extensive waves of extinction, in the cases of events impinging on many species. Examples discussed elsewhere in this volume are the terminal-Cretaceous extinction wave attributed to an asteroid impact (Raup present volume), the late-Pleistocene continental waves and the Holocene island waves that followed the first arrivals of man (Martin present volume), the late-Cretaceous plant extinctions and the late Pleistocene hominid extinctions due to evolution of competing taxa (Knoll present volume, Walker present volume), and extinctions of marine species and of swamp lycopods due to changes in climate and habitat (Stanley present volume, Knoll present volume).

At the opposite extreme are the extinctions that are constantly befalling populations isolated on islands or on disjunct patches of habitat. Such extinctions eliminate populations one-by-one rather than in a wave. They have no "cause" other than year-to-year fluctuations in the environment, or even just those accidents in the lives of individuals that may happen to eliminate all conspecifics (at least all those of one sex) on the island within a short time. Somewhere in between these two extremes lie the extinction waves due to fragmentation or insularization of habitat, as exemplified by modern extinctions in Amazonian forest fragments (Lovejoy *et al.* present volume) and post-Pleistocene extinctions in fragmented patches of montane habitat (Patterson present volume).

In this chapter I shall review the less dramatic half of the spectrum and discuss extinctions on islands or in island-like situations. This material will help us to unravel the dramatic extinctions, by showing what level of "background extinction" to expect in the absence of dramatic events. I begin by summarizing theoretical studies of what factors may determine the risk of extinction for isolated populations. There follow four sets of case studies:

1. Modern extinctions of bird populations on islands or else on mainland census plots at equilibrium, in the absence of major environmental change.

2. Modern extinctions of bird populations in habitat patches created by fragmentation of a formerly continuous habitat.

3. Extinctions of mammal, bird, and lizard populations due to late-Pleistocene fragmentation of land masses or of habitats.

4. Extinctions of species in evolutionary time, as reflected in a biota's degree of endemism.

THEORY OF POPULATION LIFETIMES

The following oversimplified summary is based on treatments by MacArthur and Wilson (1967, chapter 4), Richter-Dyn and Goel (1972), and Leigh (1975, 1981), which may be consulted for further details. Some additional complications are discussed by May *et al*. (1974).

Let us first ask how a population's probability-per-unit-time of extinction, e (in units of year^{-1}), varies with the number of individuals (or male-female pairs) in the population, N. Suppose that the probability-per-unit-time that a single individual will die is p. Then, if the deaths of individuals are independent of each other, e is simply p^N, implying a steep decline in risk of extinction with increasing population size (fig. 1). Correlations between deaths of individuals, or effects of population size on each individual's risk of death, will alter the steepness. For instance, if individuals compete with each other such that each individual's chance of dying (p) increases with population size N, the relation will be less steep. Any environmental fluctuations will also tend to make the relation less steep, since a bad year for one individual tends to be bad for all. On the other hand, mutualism, as is expected for social species, will make the relation more steep, because an individual's chance of dying decreases with population size N.

Instead of considering the probability that a population will disappear within a short time, let us now ask how long the population is expected to survive. First assume that the environment is constant, and that population fluctuations arise solely from demographic accidents (the random schedule of births and deaths of individuals). With the further assumption of geometric population growth for N less than the carrying capacity K (the maximum population size that the island can support), table 1 gives the expected lifetime T (measured in

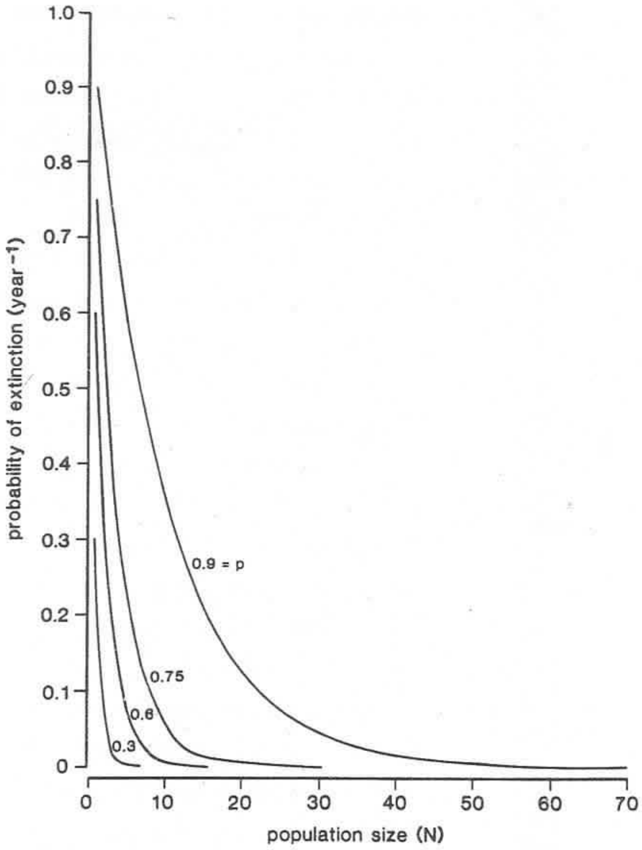


FIGURE 1. Predicted relation between the probability-per-unit time that a population will go extinct (ordinate) and the number of individuals or pairs constituting the population (abscissa). The curves are calculated as p^N, where N is the abscissa value and the number beside each curve is the value of p. This calculation in effect assumes that individuals or pairs die independently of each other with probability-per-unit time p.

generations) for a population now at K, as a function of K and of the intrinsic rate of population increase r. The lifetime is seen to increase steeply with K and with r. The proportional increase for a given K increases steeply with r, and vice versa. Since the values of table 1 are in generations

TABLE 1. Expected population lifetime. The numbers are the expected lifetime (in generations) of a population at carrying capacity, as a function of the carrying (K) and the intrinsic rate of population increase (r). The environment is assumed constant, and population fluctuations are assumed to arise solely from the random schedule of briths and deaths. Data are from table 2 of Leigh (1981). Note that expected lifetime increases with K and with r.

		K			
		10	20	30	40
r	0.1	46	197	925	4,897
	0.2	109	2,844	103,750	4,386,342
	0.3	414	92,184	29,218,650	1.057×10^{10}
	0.4	2,312	5,222,731	1.64×10^{10}	5.843×10^{13}

rather than years, a population's lifetime also increases with the generation time or lifetime of its individuals.

In fact, populations fluctuate much more widely than expected if demographic accidents were the sole cause of fluctuations. That is, the major contribution to population fluctuations comes from fluctuations of the environment. The effect of this on calculations such as those of table 1 can be obtained by assuming that environmental fluctuations yield random variation in r. With this assumption, it turns out that the higher the population's coefficient of variation (abbreviated CV), the shorter is its lifetime. The more susceptible a population is to environmental fluctuations, the more slowly its expected lifetime increases with K (Leigh 1981). For highly susceptible populations, CV becomes more important than K in determining population lifetime.

The intrinsic rate of increase r equals the difference between the instantaneous birth rate λ and death rate μ, each of which may depend on N. While population lifetime increases with r, it also increases with λ / μ. That is, the lower birth and death rates for a given difference $\lambda - \mu = r$, the safer is the population (MacArthur and Wilson 1967). Since λ, μ, r, and generation time are interrelated, the predictions for dependence of population lifetime on r, generation time, and λ/μ are also interrelated.

In short, for populations exposed to a randomly fluctuating environment rather than to occasional catastrophes, one predicts that population lifetime will increase with:

1. generation time or individual lifetime;
2. carrying capacity K or population size N, which is proportional to the product of
    - 2a. population density, times
    - 2b. island area;
3. intrinsic rate of increase r; and
4. ratio of birth to death rate λ / μ.

Population lifetime will decrease with

5. variability in population size (CV of N).

In effect, we have six separate predictions (1, 2a, 2b, 3, 4, and 5). Let us now compare these predictions with available data.

MODERN EXTINCTIONS OF BIRD POPULATIONS IN COMMUNITIES EXHIBITING TURNOVER AT EQUILIBRIUM

Numerous studies have tabulated the bird species breeding in each of a series of consecutive years on an island, or else on a mainland census plot. Some of these studies, such as the census reproduced in table 2 for Bardsey Island off the west coast of Britain from 1954 to 1969, have determined not only the breeding species in each year but also the number of breeding pairs of each species. Examples of such studies for islands are those for the California Channel Islands (Jones and Diamond 1976), the Farnes Islands off Britain (Diamond and May

1977), the Krunnit Islands off Finland (Vaisanen and Jarvinen 1977), and many British islands (Diamond 1980; Jones and Diamond, unpublished); for mainland census plots, those for Trelease Woods in Illinois (Whitcomb et al. 1976, Kendeigh 1982), seven other eastern North American woodlands (Lynch and Whitcomb 1978), northern European woodlands (Jarvinen 1979, 1980), and a British oak woodland (Williamson 1981).

All these studies have yielded the conclusion that about 1 - 30% of the breeding bird populations turn over per year on islands not undergoing marked changes of habitat. That is, bird species number in island and mainland bird communities tends to be maintained in a state of dynamic equilibrium, as a result of 1-30% of the breeding populations disappearing each year and a similar number of new populations beginning to breed or resuming breeding. Naturally, drastic habitat changes or effects of man create an imbalance between extinctions and immigrations and cause species number to change.

Such surveys permit one to calculate the probability e that a population will become extinct within one year, as a function of the average number N of pairs constituting the population during years of breeding presence. For instance, consider the five years of breeding presence documented in table 2 for the Cuckoo on Bardsey from 1954 to 1968. (We ignore the last survey year, 1969, for the purpose of this calculation, because a 1970 survey is unavailable and it is therefore unknown whether the 1969 population survived or became extinct). Of those five years, three were followed by a year of breeding absence, yielding e = 0.6 for the probability of extinction within one year. The average population size of Cuckoo in those five years was N = 1.4 pairs. Fig. 2 plots (N,e) values for all breeding species of Bardsey. It is obvious that the risk of extinction falls very steeply with increasing population size, at least as steeply as predicted by

TABLE 2. Breeding censuses of Bardsey Island. Breeding species and the number of breeding pairs are shown.

	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969
Sparrowhawk (*Accipiter nisus*)	1	1	1													
Kestrel (*Falco tinnunculus*)								1	1	1	1	1	1	1	1	1
Corncrake (*Crex crex*)	2	2														
Moorhen (*Gallinula chloropus*)	1	1	1	1	1	2	2	4	5	4	5	4	4	7	6	8
Oystercatcher (*Haematopus ostralegus*)	37	35	35	35	27	35	40	44	39	44	44	34	40	52	55	55
Lapwing (*Vanellus vanellus*)		10	8	10	8	7	20	11	10	5	4	3	6	7	6	10
Ringed Plover (*Charadrius hiaticula*)															1	1
Curlew (*Numenius arquata*)										1	1	1	1	1	1	
Wood Pigeon (*Columba palumbus*)													1		1	2
Cuckoo (*Cuculus canorus*)		1						2	1		1	2				1
Little Owl (*Athene noctua*)	3	3	3	3	4	4	5	6	7	6	5	5	5	6	6	5
Skylark (*Alauda arvensis*)	5		2	3	3	4	4	4	4	6	7	5	6	7	7	7
Swallow (*Hirundo rustica*)	10	6	6	6	6	6	6	5	4	7	5	2	4	5	7	7
Raven (*Corvus corax*)	2	3	2	3	1	2	1	3	1	1	1	2	2	3	3	2
Carrion Crow (*Corvus corone*)	3	4	4	6	7	7	6	6	4	6	5	4	4	5	4	4
Jackdaw (*Corvus monedula*)	35	30	30	25	25	30	30	20	20	25	30	50	45	50	50	47
Chough (*Pyrrhocorax pyrrhocorax*)	2	2	2	2	2	1	2	2	2	3	4	4	4	4	4	3
Wren (*Troglodytes troglodytes*)	20	19	20	20	21	30	30	20	30	4	7	10	14	20	20	20
Song Thrush (*Turdus philomelos*)					2	2	4	2				1				
Blackbird (*Turdus merula*)	3	2	2	3	2	5	7	10	14	12	12	16	16	45	47	40
Wheatear (*Oenanthe oenanthe*)	6	6	2	4	5	9	3	12	8	12	5	6	10	17	20	20
Stonechat (*Saxicola torquata*)	10	8	3	4	6	8	15	12	6	5		2	3	7	8	6
Robin (*Erithacus rubecula*)	10	7	4	1	1		3	3	3		1	1	2	2	1	
Sedge Warbler (*Acrocephalus schoenobaenus*)	2			1								1	1	1	1	1
Whitethroat (*Sylvia communis*)	5	5	5	5	7	10	15	12	14	5	5	6	6	9	10	
Willow Warbler (*Phylloscopus trochilus*)														1		
Chiffchaff (*Phylloscopus collybita*)																1
Dunnock (*Prunella modularis*)	15	13	14	15	15	15	15	15	12	5	12	13	15	20	22	35
Meadow Pipit (*Anthus pratensis*)	100	80	55	60	80	100	100	100	95	25	42	45	47	50	48	45
Rock Pipit (*Anthus spinoletta*)	50	50	50	30	20	25	25	30	30	13	20	26	20	40	40	45
Pied Wagtail (*Motacilla alba*)	3	2	3	2	2	3	2	3	3	3					1	1
Starling (*Sturnus vulgaris*)									3	3	4	12	20	21	36	50
Linnet (*Acanthis cannabina*)	35	27	20	25	27	30	30	27	30	14	20	23	15	15	15	15
Chaffinch (*Fringilla coelebs*)						1						1				
Yellowhammer (*Emberiza citrinella*)				1	2	4	4	2	3	4	4	3	4	4	3	3
Reed Bunting (*Emberiza schoeniclus*)				2	2	2	2	4	3	4	4	1	1		2	2
House Sparrow (*Passer domesticus*)	12	+	+	10	10	15	30	30	28	30	30	25	25	20	20	12
S	24	24	23	25	25	25	25	27	27	26	26	30	28	27	30	29

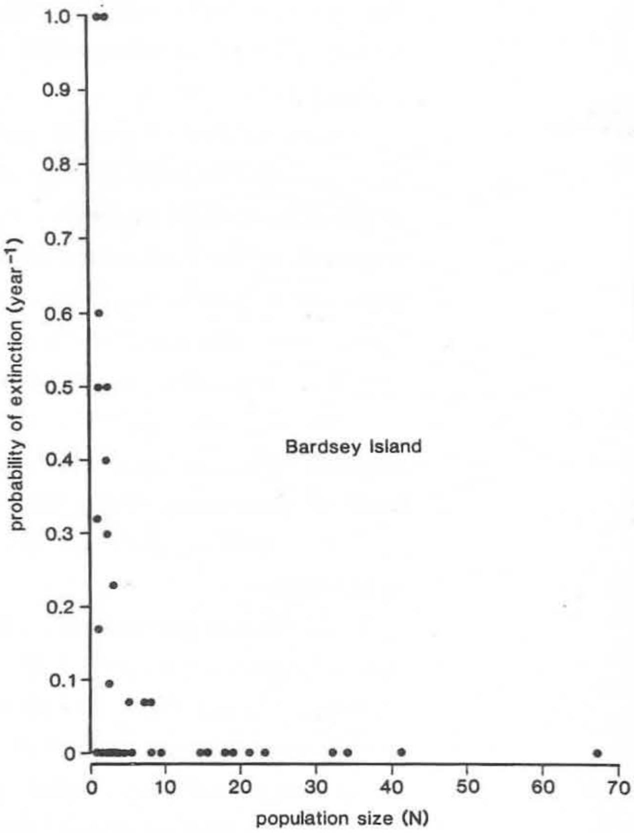


FIGURE 2. Observed relation between the probability-per-unit-time of extinction (ordinate) and the population size (abscissa), for the breeding birds of Bardsey Isle off Britain in the years 1954-1969. Compare this observed relation with the theoretical relation of figure 1. The abscissa is the average population size in years of breeding presence. The ordinate is calculated as the number of years of breeding presence that were followed by a year of breeding absence, divided by the total number of years of breeding presence. Each point represents one bird species. From analyses by H. L. Jones and J. M. Diamond, of breeding censuses evaluated by T. Reed.

the relation $e = p^N$. Similarly steep curves are obtained for 15 other British islands analyzed by Jones and Diamond (unpublished). Thus, the main predictor of extinction in these studies was small populations size. Bird censuses on the California Channel Islands yield the same conclusion (Jones and Diamond 1976, fig. 6).

Examination of graphs similar to fig. 2 for the 16 available British islands shows that certain bird species on island after island tend to have e values lying above the general pattern for their N value, while certain other species tend to have low e values for their N value on island after island. Thus, there are species-specific determinants of extinction proneness besides population size.

The species that are more extinction-prone than most other species with the same population size turn out to share one or more of four characteristics:

1. Many of them are small songbirds, which tend to be short-lived.

2. Their populations tend to fluctuate widely in abundance (year-to-year CV of $N > 0.4$: e.g., wren, lapwing, reed bunting, linnet, and whitethroat). CV was calculated as the coefficient of variation for N from consecutive surveys on an island or a mainland census plot.

3. Several of these species (wren, stonechat, song thrush) are especially susceptible to harsh winters, which may eliminate a whole population regardless of its size.

4. Several extinction-prone species of large body size (lapwing, rock dove, wood pigeon) are ones that breed in loose groups. Lack of social stimulation may make very small populations of these species prone to disappear.

Conversely, species that are more resistant to extinction than most other species with the same population size turn out to have one or both of two characteristics:

1. Most of them are large-bodied and long-lived (raven, chough, crow, moorehen).

2. Some of them have very stable populations (year-to-

year CV of N > 0.3: raven and crow).

Alternatively, one can ask which trophic category of bird species is most prone to extinction in short-term island studies. The carnivores (hawks, owls, and shrike) prove to be nearly twice as extinction-prone as the average bird species. The probable explanation is that carnivores tend to live at low population densities.

To compare different islands, one can calculate for each island the average value of the percentage of its bird populations breeding in a given year that do not breed in the following year. This value is the average per-species extinction rate e^o. If one makes comparisons among northern European islands (fig. 3) or among the California Channel Islands (Jones and Diamond 1976) or among Panamanian islands (S. J. Wright, unpublished observations), e^o is seen to decrease with island area, i.e., with increasing population sizes. In addition, e^o is seen to increase with latitude when one compares the California Channel Islands (33-34°N) with northern European islands (50-65°N), or else when one compares various mainland census plots in northern Europe (Jarvinen 1979, 1980). The likely explanation is shorter individual lifetimes at high latitudes.

Summary of turnover studies.

Turnover studies at equilibrium confirm the theoretically predicted dependences of extinction probability on population density and island area (predictions 2a and 2b). When the overriding effect of population density is taken into account, the predicted effects of individual lifetime and population variability (predictions 1 and 5) are also confirmed. Predictions 3 and 4, concerning intrinsic rate of increase r and ratio of birth to death rate λ/μ, have not been tested. The predictions concerning population density and island area have also been confirmed by turnover studies on orb spiders (Toft

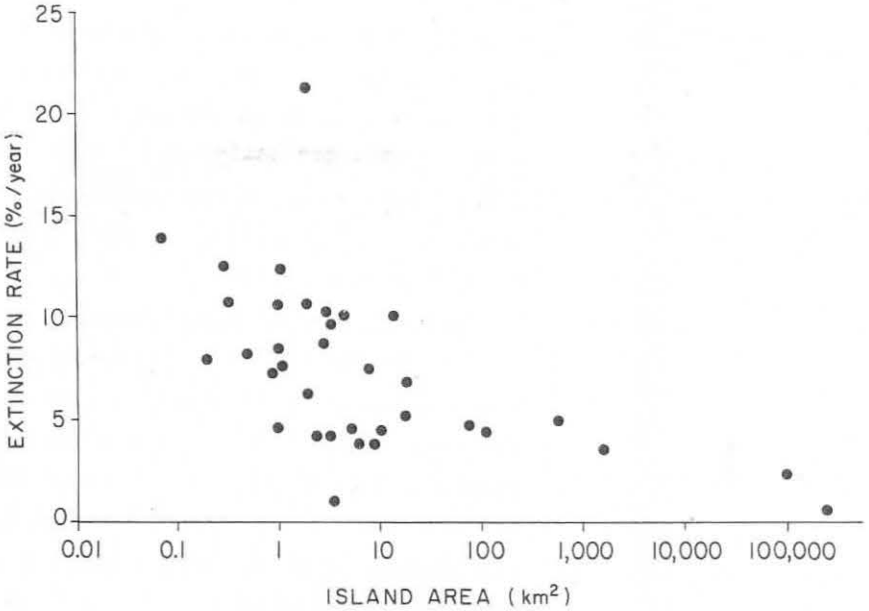


FIGURE 3. Risk of extinction as a function of island area, for breeding land birds of Northern European islands, on a time scale of one year. Ordinate: percentage of an island's breeding land bird populations that go extinct from one year to the next, on the average. Abscissa: island area. Note that risk of extinction decreases with island area. From analyses by H. L. Jones and J. M. Diamond, of breeding censuses evaluated by T. Reed.

and Schoener 1983). Comparisons of turnover studies for a range of organisms from protozoans and sessile marine organisms to arthropods, lizards, and birds show that extinction rates decrease approximately linearly with generation time (Schoener, 1983).

MODERN EXTINCTIONS OF BIRD POPULATIONS IN COMMUNITIES UNDERGOING HABITAT FRAGMENTATION

The previous section considered islands or habitat areas not undergoing drastic habitat changes, and hence maintaining species number more or less steady. In this section I instead consider habitats that are being or have recently been fragmented. Reduction in area inevitably means a net loss of species, due to an excess of extinction over immigrations. I ask: can one generalize about which species are most prone to disappear as a result of modern habitat fragmentation? Elsewhere in this volume Lovejoy _et_ _al_. discuss the effect of modern habitat fragmentation on an Amazonian rainforest biota. The present chapter considers five other such studies.

1. _Southeastern_ _Brazilian_ _woodlots_. Willis (1979, 1980) studied bird distributions in three forest tracts on the Sao Paulo plateau of southeastern Brazil. Over the past 150 years the formerly unbroken forest that covered this plateau has been largely cleared for agriculture, leaving only small and isolated forest "islands". The three tracts studied by Willis were 1,400, 250, and 21 ha in area, and supported respectively, 175, 119, and 76 breeding species as of 1975-1978. Since the original forest avifauna of the plateau consisted of about 203 species, the largest tract has lost about 28 species, the medium-sized one 84 species, and the smallest one 127 species. The large tract contains virtually all species of the medium-sized one, which in turn contains virtually all species of the small tract. Thus, the extinctions resulting from forest fragmentation occur in a fairly regular sequence.

Some groups of birds have been more extinction-prone than others. For instance, the smaller tracts have lost most species of large-bodied canopy frugivores (parrots, toucans, and cotingids), large-bodied terrestrial insectivores, and small-bodied understory omnivores and insectivores and most edge species. A generalization that makes sense of these results is that risk of extinction in the small tracts decreases with initial abundance, as assessed by current abundance in the largest tract (fig. 4). That is, the most extinction-prone species are the rarest ones (Terborgh and

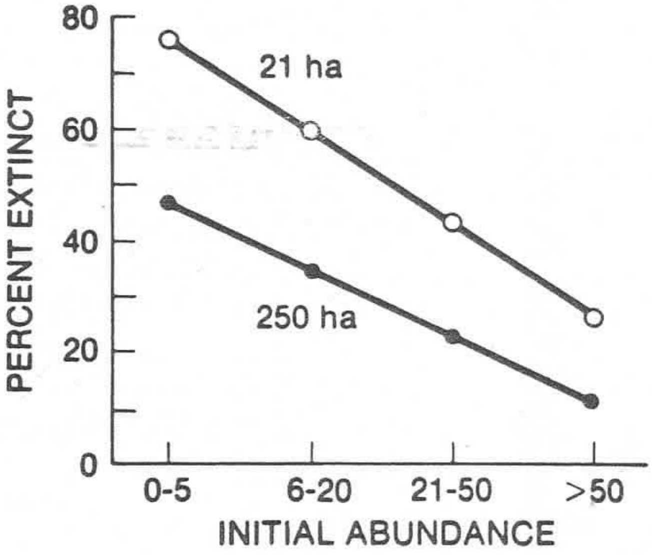


FIGURE 4. Risk of extinction as a function of population density and habitat area, for Brazilian forest birds, on a time scale of several decades. For two forest patches, one of area 21 ha, the other of 250 ha, initial population densities were estimated and expressed as bird individuals encountered per 100 hours of observation. Populations were then grouped into four classes on the basis of population density (abscissa). The ordinate gives the percentage of populations in each class that became extinct over the past few decades. Note that risk of extinction decreases with population density for each patch and is higher for the smaller patch. From Terborgh and Winter (1980), based on data of Willis (1979).

Winter 1980). In addition, forest species that readily fly across open country have been less likely to disappear in small tracts than sedentary species, presumably because populations of the former species are not truly isolated but can be replenished by colonizing individuals from other forest tracts.

2. Rio Palenque Field Station, Ecuador. Mention should be made of Leck´s (1979) study of an Ecuadorean forest patch that similarly became isolated by clearing of surrounding forest for agriculture. Of 170 forest bird species, 44 have

now disappeared, and 15 more declined and are likely to disappear. Among the lost species are nine very large birds and five other rare birds, as well as several mammalian carnivores.

3. *Barro Colorado Island*. The damming of the Chagras River to create the Panama Canal and Lake Gatun converted many former hilltops into islands in the lake. The best studied of these islands is Barro Colorado (Willis 1974, Wilson and Willis 1975, Willis and Eisenmann 1979, Karr 1982a and 1982b, Wright 1984a and 1984b). Of the ca. 108 breeding species formerly recorded on Barro Colorado, about 45 have disappeared. Many of these disappearances are due to habitat changes (forest edge and second-growth species eliminated by growth of forest). However, about 13 of these documented former residents are forest species whose disappearances cannot be attributed to habitat changes and are probably due to insularization. The actual number of species that disappeared may be as much as three times higher (Karr, 1982a), because intensive studies of Barro Colorado birds did not begin until well after Barro Colorado was transformed from a hilltop into an island. Thus, many populations are thought to have disappeared unnoticed.

How can one explain which particular species disappeared? Some of them were ground nesters and may have been eliminated by terrestrial mammalian predators, which have become abundant on Barro Colorado due to disappearance of top carnivores with large area requirements (Willis 1974, Wilson and Willis 1975, Terborgh and Winter 1980, Karr 1982a). When rarity is inferred from its correlates of large body size, high trophic level, and high metabolic requirements, extinction proneness correlates poorly with inferred rarity (Wright 1984b). For birds catchable in mist-nets, abundance measured by mist-nets is also a poor predictor of extinction (Karr 1982b). However, for the whole avifauna, relative abundances estimated by Christmas counts on the Panama mainland do have predictive value, the rarer species being more extinction-prone (Wright 1984b). For mist-netted species Karr (1984b) concluded that population variability (CV of N) predisposes species to extinction. The reason why inferred correlates of rarity are of low predictive value may be that large species at high trophic levels are not only rare; they also tend to be good overwater dispersers, hence likely to buffer their Barro Colorado populations against extinction through arrival of colonists from the Panama mainland.

4. Banks Peninsula. When European settlement of New Zealand began in the early 19th century, the forests of South Island's Banks Peninsula were already separated from the main body of South Island forest by the grasslands of the Canterbury Plains. During the late 19th century the peninsular forests were heavily logged and fragmented, until today they exist only as scattered patches, of which the largest is about 250 hectares (Johnston 1969).

Knowledge of Banks Peninsula birds has been summarized by Turbott (1969), and I am indebted to Dr. Gordon Williams for further information.

Early European ornithologists recorded about 23 species of native forest birds from the peninsular forests (table 3). Only 11 of these species persist on the peninsula today. Four of the 12 lost species disappeared completely or almost completely over the whole of New Zealand in the late 19th century, due to introduced rats, mammalian predators, and other factors. The other eight lost species are still widespread in large tracts of New Zealand forest. Their disappearances on the peninsula, mainly in the decade after 1900, coincided with the peak in forest destruction and fragmentation. Of the 11 species that survived, none is uncommon, and eight are small passerines that rank as the most abundant bird species of South Island. In contrast, six of the eight species lost through

TABLE 3. Forest birds of New Zealand's Banks Peninsula. The data are from Turbott (1969), as evaluated by G. Williams.

1. Formerly present, now absent. The populations not only of the Banks Peninsula but also over the whole of New Zealand crashed during the 19th century:

Kokako	*Callaeas cinerea*
Saddleback	*Philesturnus carunculatus*
Bush Wren	*Xenicus longipes*
Thrush (Piopio)	*Turnagra capensis*

2. Formerly present, now absent. Still widespread in large tracts of New Zealand forest:

Weka	*Gallirallus australis*
Falcon	*Falco novaeseelandiae*
Red-crowned Parakeet	*Cyanorhampus novaezelandiae*
Yellow-crowned Parakeet	*Cyanorhampus auriceps*
Kaka	*Nestor meridionalis*
Long-tailed Cuckoo	*Eudynamis taitensis*
Robin	*Petroica australis*
Yellowhead	*Mohoua ochrocephala*

3. Still present:

Pigeon	*Hemiphaga novaeseelandiae*
Shining Cuckoo	*Chrysococcyx lucidus*
Morepork Owl	*Ninox novaeseelandiae*
Rifleman	*Acanthisitta chloris*
Fantail	*Rhipidura fuliginosa*
Tomtit	*Petroica macrocephala*
Brown Creeper	*Finschia novaeseelandiae*
Grey Warbler	*Gerygone igata*
Bellbird	*Anthornis melanura*
Tui	*Prosthemadera novaeseelandiae*
Silvereye	*Zosterops lateralis*

forest fragmentation live at lower densities, possibly lower than that of any of the 11 species that survived. The disappearance of the two remaining species, the formerly common robin and yellowhead, may be somehow related to their being much more sedentary than any of the 11 survivors or than all of the other lost species except the flightless weka. Perhaps the ability to reverse extinctions in one forest patch by recolonization from other patches has been important to bird survival in the fragmented Banks Peninsula forest.

5. *Eastern North American deciduous forest.* The deciduous forests of the eastern United States have become greatly

fragmented since European settlement. Whitcomb et al. (1981) summarized extensive studies of bird distributions in relation to the area and isolation of forest fragments and the life history properties of the bird species. The authors identified a group of 15 species that are confined to the forest interior, and that in addition prove to be virtually confined to forest tracts exceeding 70 ha in area. Thus, these species tend to be eliminated by forest fragmentation. Three of them (worm-eating, hooded, and black-and-white warblers) have thus disappeared from entire 25-km^2 blocks.

The most remarkable finding is that 11 of these 15 species are long-distance migrants that winter far to the south in the neotropics and commute annually between breeding and wintering grounds! One might have guessed a priori that fragmentation would mainly affect sedentary permanent residents and least affect long-distance migrants, since vagile species are the ones that would most likely rapidly recolonize a forest patch following a temporary extinction.

Whitcomb et al. (1981) explain this paradox in two ways. First, banding recoveries show that returning adults of the long-distance migrants tend to be philopatric. Thus, the long migration flight between winter and summer grounds may be irrelevant to colonizing of new summer territories: these species are functionally sedentary if one is concerned with breeding sites. Second, philopatry also means that individuals replacing territory-holders that died since the last breeding season tend to come from nearly forest patches. For example, breeding censuses are available for Cabin John forest before and after destruction of adjacent forest. The populations of neotropical migrants increased in the year following destruction of adjacent forest (as its returning territory-holders moved to Cabin John), but then declined drastically in subsequent years due to the permanent loss of neighboring sources of colonists. In contrast, populations of permanent resident species were steady throughout this period.

Summary of modern fragmentation studies. These five studies of modern habitat fragmentation differ from the turnover studies discussed in the preceding section in an important respect. The turnover studies were concerned with year-to-year extinction, documented by absence of a breeding population of a species in a year following a year of breeding presence for the same species. The extinction was still counted as such for the purposes of the analysis even if the species then bred again the next year. In contrast, the fragmentation studies merely ask what species were present before fragmentation many years ago but are now absent. Absence now requires not only that the species have become extinct but also that it not have subsequently recolonized. Thus, species differences in persistence today cannot be be interpreted unequivocally in terms of differences in resistance to extinction: they may also mean differences in ability to recolonize.

It is certain that recolonization plays at least some role in the results of most or all of these studies. For eastern North American forest patches Whitcomb *et al*. (1981) explicitly consider species differences in recolonization as the overwhelming determinant of species differences in persistence. Recolonization was noted as the cause of some continued presences of species on the southeastern Brazilian woodlots, Barro Colorado, and Rio Palenque.

Persistence correlates with population density in four of these five studies (all except the last). It correlates with area in the Brazilian study, and inversely with population variability on Barro Colorado. The other three theoretical predictions about extinction listed earlier were not tested. The area effect in the Brazilian study is the strongest indication that at least some of the patterns reflect differing resistance to extinction, not just differing ability to recolonize. The correlation between population density and persistence is compatible with the extinction interpretation but also with an interpretation based on recolonization: abundant mainland species produce more colonists. Haila _et al._ (1979) were able to interpret species differences in persistence on Finland's Aland Archipelago on the latter basis.

In order to decide the relative importance of species differences in extinction and recolonization for interpreting these fragmentation studies, it will be necessary to identify which species are actually capable of dispersing across open country (or Lake Gatun) between forest patches. For species incapable of such dispersal, persistence does provide unequivocal evidence of resistance to extinction. Wright (1984b) has begun to analyze the Barro Colorado avifauna from this point of view.

A further consideration in these fragmentation studies concerns ways of assessing the composition of the pre-fragmentation avifauna. Clearly, the ideal way is to have available a survey before fragmentation, for the same forest patch left standing after fragmentation. Two of the eastern North American patches, Cabin John and Trelease Woods, were actually surveyed yearly for several decades, and World Wildlife Fund is now doing so for Amazonian patches under study (Lovejoy _et al._ present volume). Multiple surveys are also available for Barro Colorado and Rio Palenque, but many species may have disappeared from both in the early years of fragmentation, before surveys began (Karr 1982a). When a pre-fragmentation survey for the patch itself is not available, there are two alternative ways to assess the pre-fragmentation fauna: to equate it with the pre-fragmentation fauna of a larger region including the patch, as available for the southeast Brazilian and Banks Peninsula studies; or to equate it with the fauna of a much larger forest in the vicinity today, as Whitcomb et al. (1981) did for some eastern North American patches. Both of these alternatives are imperfect, in that a small patch would not start out with all the species of a larger tract in which it was embedded. However, one can calculate the magnitude of this error from the so-called continental species/area relation for the fauna and region studied (a graph of species number against area for nested census areas).

EXTINCTIONS OF MAMMAL POPULATIONS ON LAND-BRIDGE ISLANDS AND MONTANE COMMUNITIES FRAGMENTED AT THE END OF THE PLEISTOCENE

The end of the Pleistocene fragmented species ranges in two ways. First, sea level rose more than 100 m due to glacial melting, converting coastal lowlands into shallow seas and thereby dissecting many land masses. Examples include the dissection of Britain from Europe, of Trinidad from South America, of Fernando Po from Africa, of Tasmania from Australia, and of Ceylon, Japan, Taiwan, Hainan and the Greater Sunda Islands from Asia (figs. 5, 8, 11, 13). More than a century ago Alfred Russel Wallace recognized that the presence of flightless mammals and other taxa with poor water-crossing ability on these islands was a legacy of the now-submerged Pleistocene land bridges. For instance, it was over such a bridge that rhinoceroses walked to what is now the island of Java.

Second, late-Pleistocene rising temperatures and altered rainfall patterns fragmented continental expanses of habitat into habitat patches. For example, habitats now distributed disjunctly on mountain tops were continuous at lower elevations during cool periods of the Pleistocene. The mystery of how the same species of flightless montane animals and plants with heavy seeds came to occupy the tops of distant mountains, such as the Pyrenees and Alps and Caucasus, was solved by Forbes

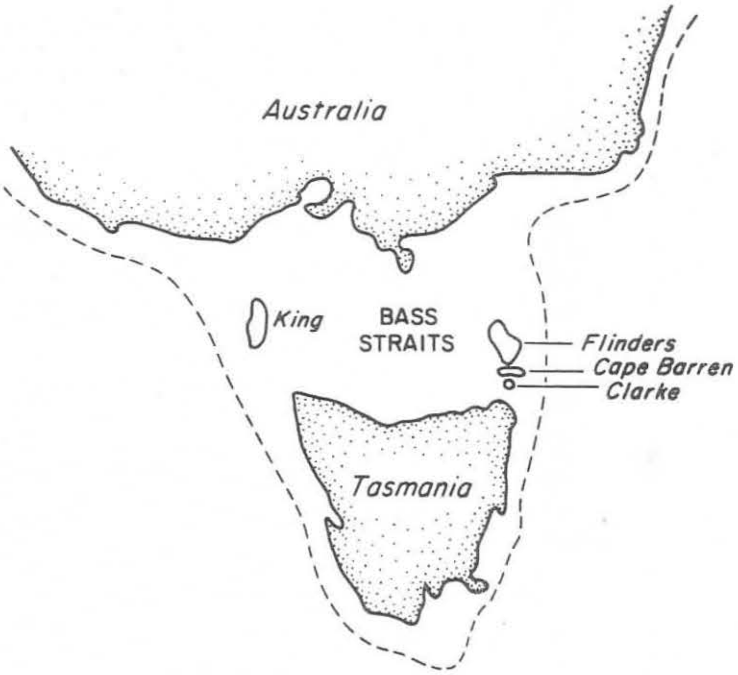


FIGURE 5. Map of Bass Strait, which separates Tasmania from Australia today. The dashed line represents the coast line at Pleistocene times of low sea level, when Bass Strait was dry land and Tasmania was part of the Australian mainland. Rising sea level flooded most of the Bass Strait platform except for the highest hills that became modern islands, with the result that Tasmania is now cut off from Australia.

(1846), who pointed out that dispersal had formerly been possible.

These late-Pleistocene fragmentations of land masses and habitats sundered species ranges. Some of the resulting fragments retained more of their initial biota than did others, and some species survived on more fragments than did others. Post-Pleistocene extinctions have either been documented directly by fossil remains of species at a site where the species no longer occurs, or else inferred from modern discontinuous distributions. Such studies are available for mammals, birds, and lizards. I begin with the mammal studies, because they are easier to interpret for two reasons. First, fossil evidence is far better for mammals than for birds and lizards, so that mammal extinctions are often documented rather than inferred. Second, the poorer dispersal abilities of mammals permit one to be more confident that modern disjunct distributions are the product of differential extinction alone, not of extinctions partly reversed by immigrations. I shall discuss three sets of studies for mammals.

1. *Tasmania and the Bass Strait islands*. Bass Strait, which now separates Tasmania from Australia, nowhere exceeds 100 m in depth. Thus, the entire strait was a land platform at low-sea-level times of the Pleistocene (fig. 5). Rising sea levels submerged most of this platform, leaving one large island (Tasmania, 67,900 km^2), four islands of 100 to 1,500 km^2 (Flinders, King, Cape Barren, and Clarke), and many smaller islands. Hope (1973) has reported the extant and recent fossil mammals of these islands. Her study is a particularly clean study of differential extinction, because there is fossil evidence for former presence of almost all modern Tasmanian mammal species on smaller islands now lacking those mammals; the fossils permit approximate dating of some of the extinctions; the approximate time when various land connections were severed is known; and humans were among the first species to disappear on all islands except Tasmania, so that extinctions of other mammals due to fragmentation are not confounded by effects of man. In addition, most of the modern water gaps are too wide to be crossed by most of the mammal species involved, so that modern presence of a mammal on many islands implies resistance to post-Pleistocene extinction rather than good overwater colonizing ability.

The largest island (Tasmania, 67,900 km^2), second largest (Flinders, 1,330 km^2), and third largest (King, 1,110 km^1)

retained respectively the most (25), second most (13), and third most (12) native flightless mammal species. Fig. 6 shows that the number of herbivorous marsupials increases with island area: Tasmania retained 10 species, the four islands in the size range 100-1,500 km^2 retained 4-7, most islands of 1.4 to 10 km^2 retained 1 or 2, and no island smaller than 1.4 km^2 retained any.

Species varied greatly in their resistance to extinction following habitat fragmentation (fig. 7). Species confined to a few islands are generally on the largest islands, while those on many islands are also on numerous small islands. At one extreme, the rat-kangaroo Aepyprymnus rufescens and the mouse Pseudomys novaehollandiae disappeared from all islands and

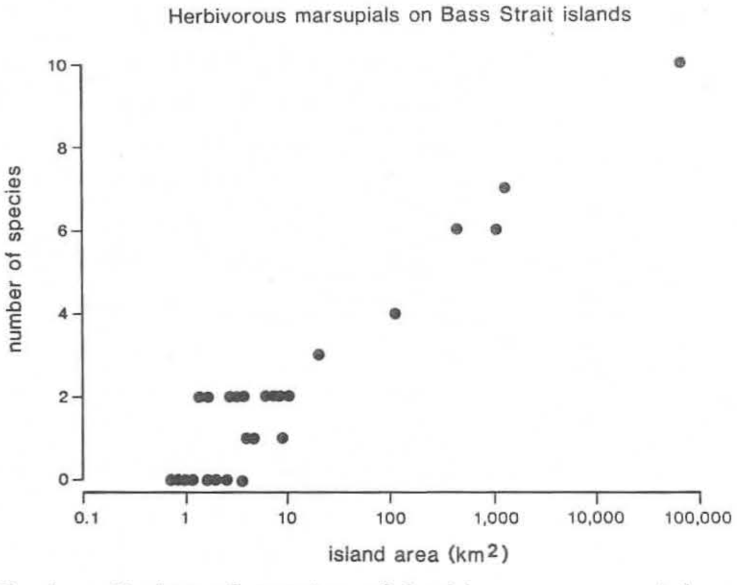


FIGURE 6. Number of species of herbivorous marsupials on the islands of Bass Strait in modern times, as a function of island area. Note that species number increases with island area, so that the largest island (Tasmania) has 10 species while islands smaller than 1.4 km^2 have no species. Data are from Hope (1973). The pattern was produced by differential extinction, small islands suffering more extinctions than large islands.

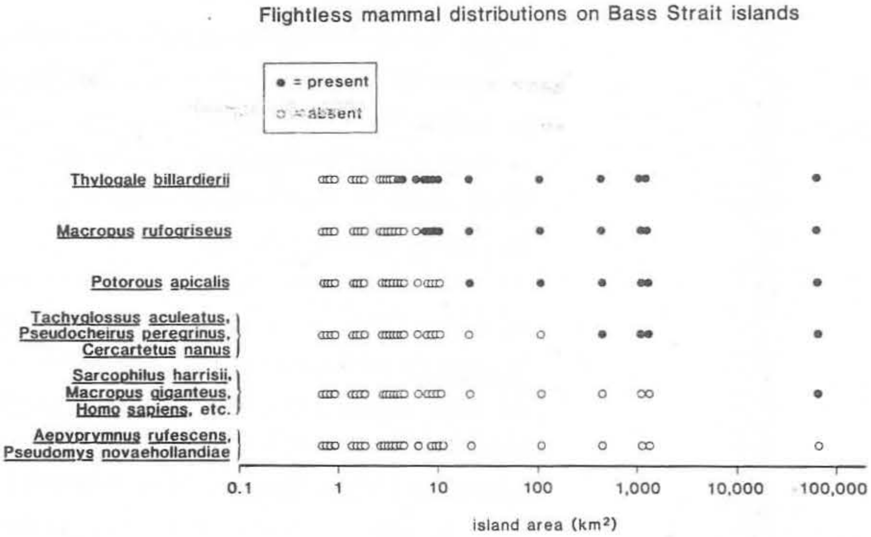


FIGURE 7. Distributions of the flightless mammals named on the left, on islands of Bass Strait, as a function of island area. Species tend to be distributed from the largest island down to islands of a lower size limit that varies with the species. The species that occupies the largest number of islands and that reaches the smallest islands is at the top, while the next to the bottom line depicts species confined to the largest island (Tasmania), and the bottomline depicts two species that disappeared from all the islands and are now confined to the Australian mainland. Data are from Hope (1973). This pattern was produced by differential extinction, some species being more susceptible than others.

survived only on the Australian mainland. The marsupial "cat" Dasyurus viverrinus, Homo sapiens, and nine other species did little better, surviving on Tasmania and no other island. At the opposite extreme, the wallaby Thylogale billardierii survived on 17 islands, including one of only 1.4 km^2.

How can one explain why some mammals were so much more susceptible to effects of habitat fragmentation than were others? Three generalizations emerge:

(a) Carnivores were more susceptible than herbivores. Among mammals weighing over 1 kg, three of the four marsupial carnivores (the Tasmanian "wolf" Thylacinus cynocephalus, the Tasmanian devil Sarcophilus harrisii, and Dasyurus viverrinus) survived only on Tasmania, while seven of the nine marsupial herbivores in this weight range survived on 5-17 islands, including islands as small as 1.6 or 1.4 km^2.

(b) Large carnivores were more susceptible than small carnivores. The largest carnivores (T. cynocephalus and S. harrisii) survived only on Tasmania, while the smallest carnivores (Smithopsis leucopus and Antechinus minimus) survived on islands as small as 6 and 9 km^2, respectively. The omnivorous Homo sapiens, the largest flightless mammal of Bass Strait, also survived only on Tasmania. (The Tasmanians lacked watercraft capable of voyages exceeding a few miles). For herbivores, however, there is not a clear inverse relation between survival and size. For instance, the third and fourth largest herbivores, the wallabies Macropus rufogriseus and Thylogale billardierii, are the ones on the largest number of islands (11 and 17, respectively), far more than species one-tenth their weight.

(c) Habitat specialists were more susceptible than habitat generalists. Two small rodents of specialized habitats, Mastacomys fuscus and Pseudomys higginsi, survived only on Tasmania. The platypus Ornithorhynchus anatinus, which is confined to fresh water, survived on only Tasmania and two other large islands.

Thus, the main pattern visible for Bass Strait Mammals is that risk of extinction decreased with inferred population size. This is why large islands retained more species than small islands; why herbivores, habitat generalists, and small carnivores survived on more islands than did carnivores, habitat specialists, and large carnivores; and why the latter three types of species, which tend to live at low population density, survived usually just on the largest island(s).

2. Islands of the Sunda Shelf. It was the rhinoceroses of Java and Sumatra that brought Alfred Russel Wallace to appreciate the importance of former land connections for the modern distributions of species blocked by water gaps. Java, Sumatra, Borneo, and many adjacent smaller islands are separated from each other and the Asian mainland by the shallow waters of the Java Sea and South China Sea. In the Pleistocene the entire Sunda Shelf was an extension of the Asian mainland. Rising sea-level fragmented the shelf into its modern configuration of sea and islands (fig. 8).

Fig. 9 (from Wilcox 1980) depicts the number of flightless extant mammal species, S, as a function of island area for the islands of the Sunda Shelf. For all islands S is lower than in an equivalent area of the adjacent Asian mainland. The smaller the island, the lower is the proportion that the island's mammal fauna bears to the continental fauna of an equivalent area. This suggests that post-Pleistocene extinctions have proceeded further on the small islands than on the large islands. This interpretation is confirmed for 10 big mammals of the Greater Sunda Islands by fossil evidence. Today these 10 mammals (tiger, orangutan, Javan and Sumatran rhinoceroses, elephant, gibbon, banteng, leopard, Malay tapir, and Malay bear) are patchily distributed on the three largest islands (Borneo, Sumatra, Java), each species being on only one or two of the three islands. Of 30 possible populations (3 species x 10 islands), only 17 are extant. However, in nine of the 13 cases of species presently missing, the species is known as a Pleistocene fossil from the same island (Hooijer, in Terborgh 1974). Thus, modern absence does mean past extinction rather than non-arrival.

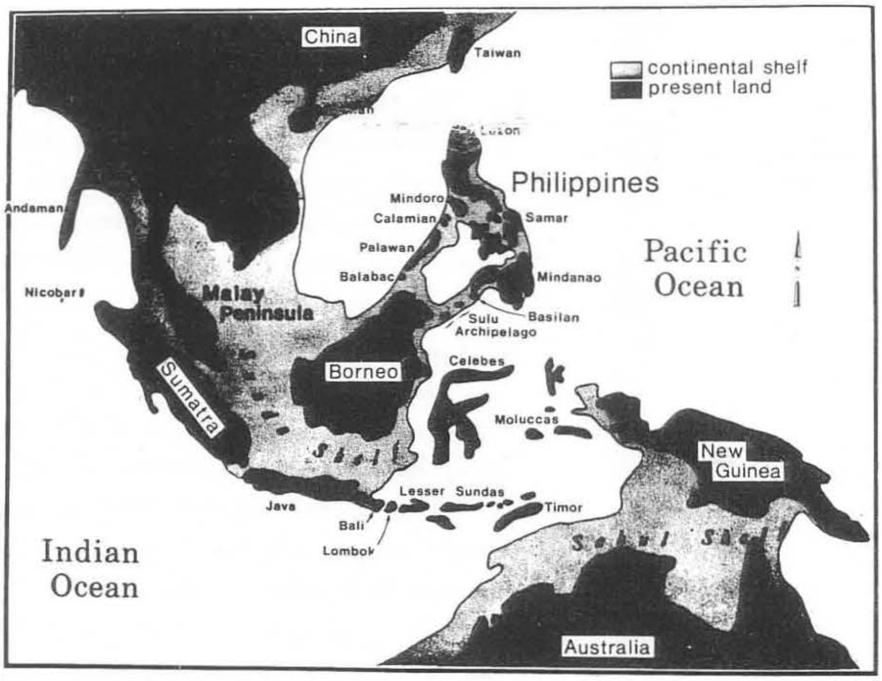


FIGURE 8. Map of the region from Southeast Asia to Australia, depicting modern land configurations today as well as land configurations at Pleistocene times of low sea level. Sea-level lowering converted the Sunda Shelf into an extension of Southeast Asia, and joined New Guinea, Australia, and the Sahul Shelf into a single continent. Rising sea level fragmented both shelves into archipelagoes of islands and separated New Guinea from Australia.

A systematic analysis to evaluate which species were most susceptible to extinction has not been done. It is obvious that some small mammals fared much better than any of the 10 just-mentioned big mammal species. None of the 10 big mammals managed to survive even on all three of the largest islands. In contrast, some squirrels and other small mammals survived not only on all three of the largest islands but also on islands that were too small to retain any of the big mammals.

3. Mountains of western North America. During cool periods of the Pleistocene, habitats today confined to higher

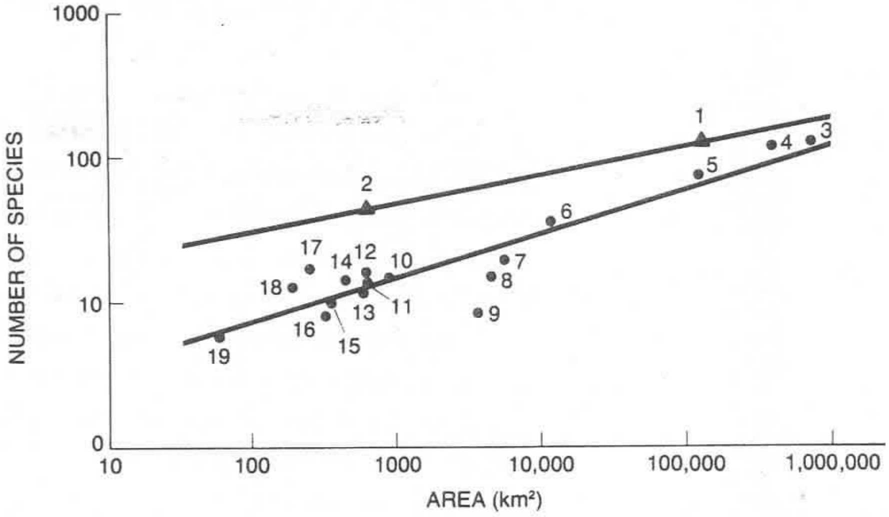


FIGURE 9. Lower line and points: the species/area relation for flightless mammals on islands of the Sunda Shelf, which was part of the Asian mainland at Pleistocene times of low sea-level. Upper curve and points: species/area relation for flightless mammals on pieces of the Southeast Asian mainland of varying areas. As a result of post-Pleistocene extinctions, S on all islands today is lower than in an equivalent area of the Asian mainland, and the smaller islands have lost proportionately more of their original mainland fauna and contain a lower proportion of the mammal fauna found in an equivalent mainland area. From Wilcox (1980); see Wilcox for identification of islands and mainland areas by number.

elevations of western North American mountains extended to lower elevations and lower latitudes. Flightless mammals characteristic of these habitats were then able to occupy the basin floors and to disperse among mountain ranges. Rising temperatures drove the habitats and their mammals up the mountains, leaving them unable to disperse through the deserts of the basin floor and yielding the disjunct distributions that we see today. The isolated populations were then subjected to a process of differential extinction. Fossils confirm the former presence of montane mammal species in lowland or southern areas or on certain mountains where the species no longer occur today.

Two sets of studies have been carried out on this differential extinction of montane mammals. Elsewhere in this volume Patterson reports his studies for 28 ranges of the southern Rocky Mountains. His results agree with and extend those of Brown (1971, 1978) for 19 ranges of the Great Basin. Brown´s findings will be summarized here.

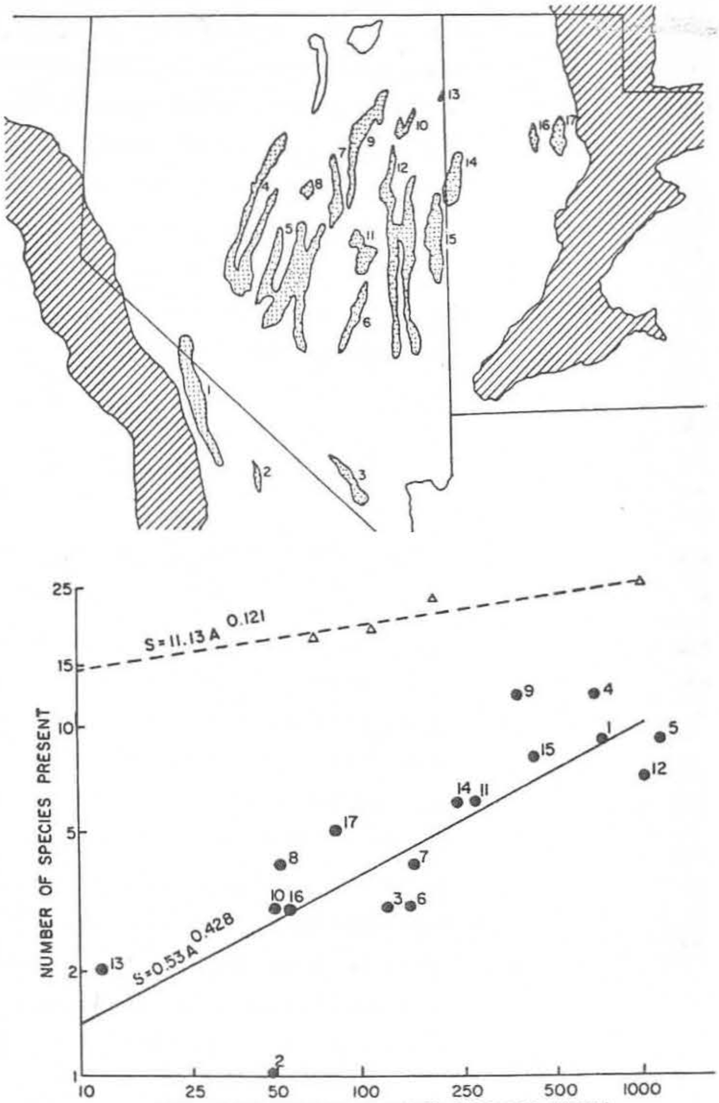
The montane mammals on the isolated mountain "islands" of the Great Basin are ultimately derived from the much larger "mainland" mountain ranges of the Sierra Nevadas to the west and of the Rocky Mountains to the east (fig. 10). Fig. 10 demonstrates, as did fig. 9 for the islands of the Sunda Shelf, that the number of montane mammal species on an isolated mountain range is lower than in a comparable area of the Sierra Nevada "mainland". The smaller the mountain, the lower the proportion that its mammal fauna bears to that in an equivalent Sierran area. This implies that extinction has proceeded further on the smaller mountains.

Table 4 shows that some species fared much better than did others. The chipmunk _Eutamias umbrinus_ survived on 17 of 19

FIGURE 10. Above: map of the Great Basin of western North America, outlining mountain ranges at the 7500-ft. contour. The Great Basin today consists of mountain "islands" separated by deserts of the basin floor. Below: species/area relation for small flightless montane mammals on mountains of the Great Basin (lower curve), and for sample areas of various sizes in the continuous plateau of the Sierra Nevada (upper curve). As a result of extinction since the Pleistocene, the mountain "islands" contain fewer mammal species than equivalent Sierran areas, and the smaller mountain ranges have lost proportionately more species than the large ranges. From Brown (1971): see Brown for identification of "islands" and "mainland" areas by number.

Montane Mammal Species

on "Mountain Islands" of the Great Basin



mountains (all but the two smallest mountains), while the hare Lepus townsendi survived only on a single large mountain. Three generalizations emerge. Habitat specialists (labelled S in table 4), confined to streams, meadows, or rock piles, fared much worse than did habitat generalists of similar size and trophic status. Habitat generalist carnivores fared worse than did habitat generalist herbivores of similar size. Big mammals tended to fare worse than did small mammals of similar trophic status and habitat preference.

The preferential extinctions of populations on small mountains, and the preferential extinctions of carnivores, habitat specialists, and large mammals, all fit the pattern that risk of extinction decreases with inferred population size. These same four patterns describe Patterson´s (present volume) study for the southern Rocky Mountains.

EXTINCTIONS OF BIRD POPULATIONS ON LAND-BRIDGE ISLANDS FRAGMENTED AT THE END OF THE PLEISTOCENE

Flightless mammals are obviously suitable for studies of differential extinction on land-bridge islands, because their water-crossing abilities are so obviously poor. It may at first seem surprising that comparable analyses could be carried out for birds at all. Since most birds can fly, one might expect extinction of a bird population on a land-bridge island to be highly susceptible to reversal by subsequent overwater colonization. Thus, one might think that modern presences of birds on land-bridge islands would reflect overwater colonization ability as much as resistance to extinction and therefore could not yield unequivocal conclusions about extinction.

At the level of an entire avifauna, this reasoning is correct. However, some bird species (and also some bat species) that are capable of flight nevertheless refuse to cross water gaps (Diamond 1976, 1981). Such species afflicted

TABLE 4. Differential extinction of mammals due to post-Pleistocene habitat fragmentation. Modern distributions of small flightless mammal species of pinon-juniper woodland, on 19 mountain ranges rising from the Great Basin of western North America. Woodland is now disjunctly distributed on montane "islands" above 7500 feet, separated by deserts of the basin floor. During cool wet periods of the Pleistocene the woodlands were continuously distributed across the basin, and small mammals could disperse between mountains. Habitat fragmentation since the Pleistocene has subjected mammal populations to differential extinction, resulting in modern absences of many species from many mountains. The body weight, diet (H = herbivore, C = carnivore), and habitat preference (G = habitat generalist; S = confined to a specialized habitat such as streams, meadows, or talus) are given for each species. Note that large animals, carnivores, and habitat specialists disappeared on more islands (-), especially on the smaller islands, than did small animals, herbivores, and habitat generalists. That is, rare animals were more prone to extinction following habitat fragmentation than were common animals. Large habitat islands (last row: area) retained more species (next-to-last row) than did small islands. From Brown (1971, 1978).

					Mountain Ranges																		
Species	Number of islands per species	Weight (in grams)	Diet	Habitat	Toiyabe	Ruby	White-Inyo	Snake	Toquima	Schell Creek	Deep Creek	White Pine	Desatoya	Spring	Stansbury	Oquirrb	Grant	Diamond	Spruce	Roberts Creek	Sheep	Pilot	Panamint
Eutamias umbrinus	17	60	H	G	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-
Neotoma cinerea	17	300	H	G	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	-	+	+	+
Eutamius dorsalis, *E. panamintinus*	16	55	H	G	+	-	+	+	+	+	+	+	-	+	+	+	+	+	+	-	+	+	+
Spermophilus lateralis	14	170	H	G	+	+	+	+	+	+	+	+	+	+	-	-	+	+	+	-	-	+	-
Microtus longicaudus	13	45	H	G	+	+	+	+	+	+	+	+	+	-	+	+	+	-	-	+	-	-	-
Sylvilagus nuttallii	12	800	H	G	+	+	+	+	+	+	+	+	+	+	-	-	+	-	-	-	-	-	+
Marmota flaviventris	10	3,000	H	G	+	+	+	+	+	+	+	+	+	-	+	-	-	-	-	-	-	-	-
Sorex vagrans, *S. tenellus*	8	7	C	G	+	+	+	+	-	+	+	-	-	+	-	+	-	-	-	-	-	-	-
Sorex palustris	6	14	C	S	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Ochotona princeps	5	120	H	S	+	+	+	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Zapus princeps	4	25	H	S	+	+	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-
Mustela erminea	4	50	C	G	+	-	+	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
Spermophilus beldingi	3	300	H	S	+	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lepus townsendii	1	3,000	H	S	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
number of species per mountain					13	12	11	10	10	8	8	7	7	6	6	6	5	4	4	4	3	3	3
mountain area above 7500 feet (sq. miles)					684	364	738	417	1178	1020	223	262	83	125	56	82	150	159	49	52	54	12	47

by fear of flying overwater constitute an increasing percentage of avifaunas as one approaches the equator. The non-water-crossers represent only a few percent of northern European birds, about 20% of southern California birds, and the majority of New Guinea birds. There are hundreds, perhaps thousands of tropical bird species that live in coastal lowlands but have never been recorded from any island lacking a Pleistocene land bridge to the mainland: not even from islands only a few miles offshore. These species include all broadbills (Eurylaimidae), malkohas (Phaenicophaeus), pheasants, partridges, forktails, whistling thrushes, and song babblers of tropical Asia, and most or all species of the families Furnariidae, Formicariidae, Dendrocolaptidae, Pipridae, Bucconidae, Ramphastidae, and Galbulidae in the New World tropics. The non-water-crossers are as dependent on land bridges for access to islands, and as suitable material for study of differential extinction, as are rhinoceroses. MacArthur et al. (1972) and Diamond and Gilpin (1983) discuss criteria for identifying non-water-crossing species in the avifauna of Panama and the Malayan subregion, respectively.

I shall summarize two studies of the effects of post-Pleistocene fragmentation on birds, and briefly mention some other such studies.

1. Solomon Islands. In the northern chain of the Solomon Archipelago in the tropical southwest Pacific, all islands from Buka and Bougainville through Shortland, Fauro, Choiseul, and Ysabel to Ngela (Florida) and possibly Guadalcanal are separated today by shallow water gaps and were joined into a single huge island ("Greater Bukida": fig. 11) in the Pleistocene (Diamond and Mayr 1976, Diamond 1983). There are numerous other Solomon islands that were not connected to Greater Bukida, some of them over 3000 km^2 in area and separated from Greater Bukida by water gaps of less than 20 km.

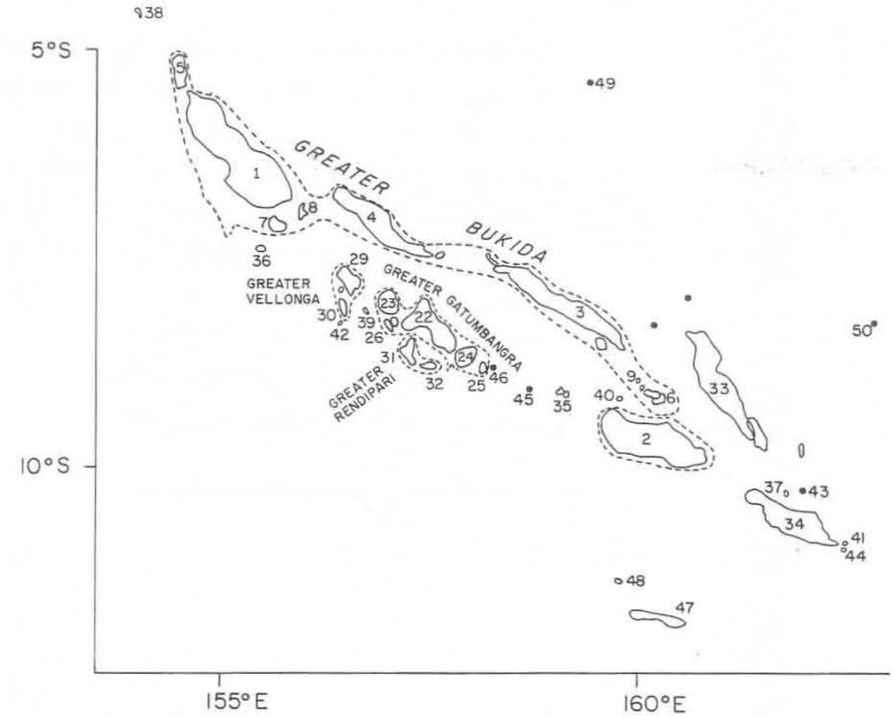


FIGURE 11. Map of the Solomon Archipelago in the Southwest Pacific Ocean, showing modern island outlines (solid lines) and also island outlines at Pleistocene times of low sea level (dashed lines). Sea-level lowering converted what are today shallow straits into dry land, joining numerous sets of modern islands into single larger islands. Rising sea level then fragmented the Pleistocene islands. The largest of these Pleistocene islands was Greater Bukida, whose fragments today extend from Buka Island in the northwest to Ngela (Florida) and possibly Guadalcanal in the southeast. From Diamond (1983); see Diamond and Mayr (1976) for identification of islands by number.

Not surprisingly, the endemic giant rats (Uromys and Solomys) of the Solomons are confined to the largest islands derived from Greater Bukida. Most Solomon bird and bat species cross water readily and occur not only on Greater Bukida fragments but also on other islands. However, 13 bird species endemic to the Solomons, as well as the endemic bats Pteralopex atrata, Pteropus mahaganus, and Anthops ornatus, are now confined to one or more islands that represent fragments of Greater Bukida. These species are evidently unable (in the case of one flightless bird species) or unwilling (in the case of the bats and the other birds) to cross water gaps. They must have been distributed over Greater Bukida when it was a single land mass. Their present distributions (summarized in table 5 for the birds) reflect the extent to which they have become extinct on the fragments of Greater Bukida in the ca. 10,000 years since it was dissected by rising sea-level. Table 5 yields the following conclusions:

TABLE 5. Distribution of land-bridge relict bird species on the post-Pleistocene fragments of Greater Bukida, Solomon Islands.

Island	Area (km^2)	Halcyon leucopygia	Zosterops metcalfii	Corvus woodfordii	Nesoclopeus woodfordi	Pitta anerythra	Accipiter imitator	Nesasio solomonensis	Halcyon bougainvillei	Rhipidura drownei	Pachycephala implicata	Stresemannia bougainvillei	Meliphaga inexpectata	Microgoura meeki
Bougainville	8591	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		
Guadalcanal	5281	✓		✓	✓				✓	✓	✓		✓	
Ysabel	3877	✓	✓	✓	✓	✓	✓	✓						
Choiseul	2966	✓	✓	✓	✓	✓	✓	✓						✓
Buka	611		✓	✓										
Ngela	368	✓	✓											
Shortland	233		✓	✓										
Wagina	90.7			✓										
Fauro	69.6	✓												
Buena Vista	14.0	✓												
Molakobi	7.67		✓	✓										
Fara	7.25	✓												
Arnavon	5.65													
Bates	5.23		✓											
Piru	2.95													
Oema	2.85													
Nusave	0.534													
Bagora	0.326													
Nugu	0.149													
Samarai	0.091													
New	0.071													
Dalakalonga	0.067													
Elo	0.055													
Kukuvulu	0.040													
Tapanu	0.0161													
Kanasata	0.0091													
Near New	0.0070													

The number of relict populations rises steeply with increasing island area, until the largest island (Bougainville, 8590 km^2) has all but two of the 13 relicts (fig. 12). Islands of 250-650 km^2 retained only two relicts. Not a single relict population survived on any of the numerous ornithologically explored Greater Bukida fragments of less than 5 km^2.

Some species are much more prone to extinction than others, even after we remove from consideration the ground pigeon Microgoura meeki (whose distribution may have become restricted by feral cats before ornithological exploration began) and the five montane species Meliphaga inexpectata, Stresemannia

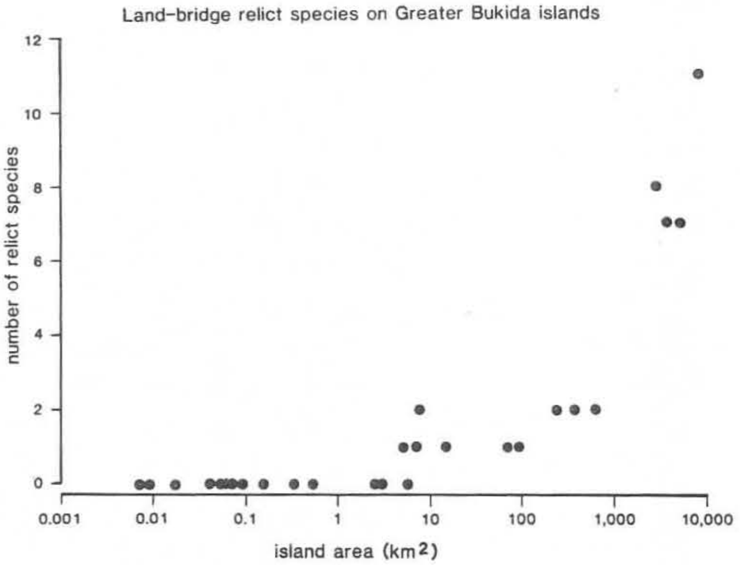


FIGURE 12. Species/area relation for land-bridge relict bird species on modern Solomon islands derived from fragmentation of the large Pleistocene island Greater Bukida by rising sea level. The ordinate gives for each island the number of bird species that are unwilling or unable to fly across water gaps and that are confined to islands derived from Greater Bukida. The populations of these bird species today are relicts of populations distributed over Greater Bukida during the Pleistocene period (Diamond 1983).

bougainvillei, *Pachycephala implicata*, *Rhipidura drownei*, and *Halcyon bougainvillei* (now confined to either or both of the two islands with the highest mountains, but possibly also formerly on medium-high islands when Pleistocene cool climates lowered the altitudinal limits of montane vegetation). Of the remaining seven species, four (the rail *Nesoclopeus woodfordi*, the pitta *Pitta anerythra*, the hawk *Accipiter imitator*, the large owl *Nesasio solomonensis*) are now confined to three or all four of the four islands with areas exceeding 2500 km^2. Three species (the kingfisher *Halcyon leucopygia*, the white-eye *Zosterops metcalfii*, the crow *Corvus woodfordi*) have survived on eight islands each, including most islands with areas of 230 km^2 or greater plus a few islands with areas of 5-90 km^2. The former four species, which must be considered extinction-prone, have considerably lower population densities than any of the latter three species, which are evidently more resistant to extinction.

The increase in species retained per island with island area, and the increase in surviving populations per species with abundance, both mean that risk of extinction decreases with population size.

2. *New Guinea land-bridge islands*. New Guinea and Australia lie on the Sahul Shelf (fig. 13). Today the shallow Arafura Sea separates New Guinea from Australia. However, at late-Pleistocene times of low sea level New Guinea, Australia, and the whole Sahul Shelf were a single land mass that was then dissected by rising sea level. Of the modern islands near New Guinea, some (e.g., Aru, Japen, Misol) are land-bridge islands that were just pieces of the New Guinea mainland until they became dissected away. Others (e.g., Biak, New Britain, Ceram) are "oceanic" islands that have had no recent land connections to New Guinea.

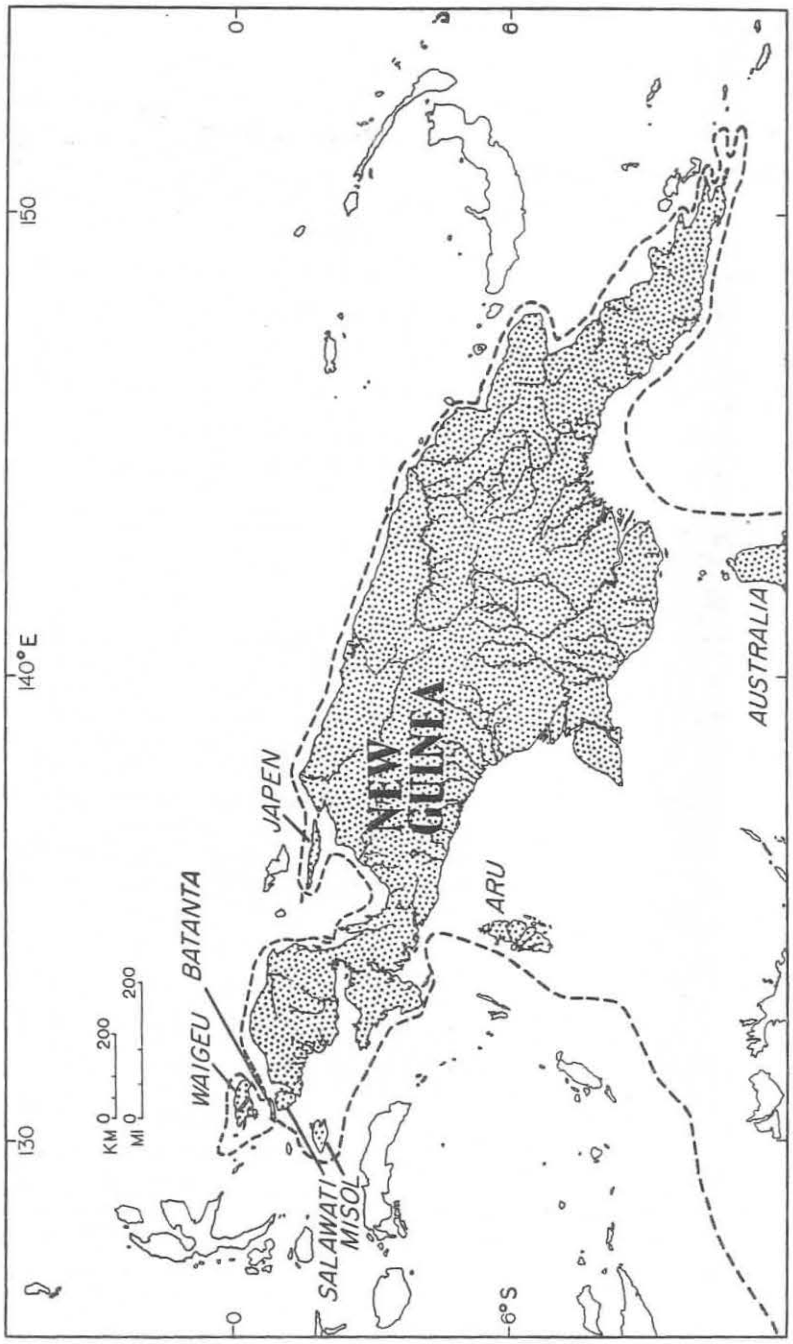
Fig. 14 shows that all the large land-bridge islands (open circle) have about twice as many lowland species as oceanic islands of comparable area and proximity to New Guinea (filled circle), but many fewer species than equal-sized pieces of the New Guinea mainland (X) (Diamond 1972). The excess of species over the number on oceanic islands arose because the land-bridge islands started off with the full species complement of the mainland. The species deficit compared to modern mainland areas arose because populations that died out after the land bridges were severed either could not be restored at all (in the case of non-water crossing species), or else had to be restored by colonization overwater rather than from adjacent mainland areas (in the case of water-crossing species). On the smallest land-bridge island ($A=0.93$ km^2) the species number is no larger than on a comparable-sized oceanic island (see last sentence of next paragraph for explanation).

Alternatively, one can focus on those 134 New Guinea lowland species that are incapable of crossing water gaps. These species occur today only on land-bridge islands, not on oceanic islands. However, their number decreases sharply with area of land-bridge island: 36-45 such species on land-bridge islands of area 1,600-7,800 km^2; 26 on an island of 450 km^2; 3 on an island of 145 km^2; and none on an island of 0.93 km^2 (which nevertheless has 14 water-crossing species). The explanation is that extinction rates increase with decreasing island area, hence all Pleistocene bird populations have disappeared in the past 10,000 years on very small land-bridge islands. Their avifauna consists entirely of post-Pleistocene overwater colonists, and their species composition as well as species number are indistinguishable from those on comparable-sized oceanic islands.

Among the non-water-crossing species, some fared much better than others on land-bridge islands since the end of the

Pleistocene. At the on extreme (fig. 13), some species, such as the black cockatoo *Probosciger aterrimus* and frilled monarch *Monarcha telescophthalmus*, have survived on all seven land-bridge islands exceeding 450 km^2 in area (but none smaller). At the opposite extreme, 32 species disappeared from all land-bridge islands, including the largest island (7,800 km^2). Most of these 32 species fit into one or more of four categories: (a) big birds with enormous territories, hence small initial populations. Examples: the New Guinea harpy eagle (*Harpyopsis novaeguineae*), Doria's goshawk (*Megatriorchis doriae*), Pesquet's parrot (*Psittrichas fulgidus*). (b) Small birds that occur in forest but are rare, hence small initial populations. Examples: the cuckoo-shrike *Campochaera sloetii*, flycatcher *Monarcha rubiensis*, and honey-eater *Timeliopsis griseigula*. (c) Non-forest species with specialized habitat requirements, hence small initial populations. Examples: the rail *Megacrex inepta*, wren-warbler *Malurus alboscapulatus*, and whistler *Pachycephala aurea*. (d) Species that depend for food on patchy and ephemeral fruits, seeds, and flowers, hence populations fluctuate greatly. Examples: the cuckoo *Eudynamis parva*, the honey-eater *Meliphaga flavirictus*, and four species of grass-finches (*Lonchura*).

FIGURE 13. Distribution of the flycatcher *Monarcha telescophthalmus* (shaded islands). The dashed line outlines the Sahul Shelf, which was all dry land at Pleistocene times of low sea level. Rising sea level fragmented the shelf into islands, isolating populations of flightless animals and birds unwilling to fly across water. The flycatcher *Monarcha telescophthalmus* today occurs on every large island fragmented from the Sahul Shelf, but on no small fragment (as a result of its extinction on small islands), nor on oceanic islands off the Sahul Shelf (as a result of its inability ever to reach these islands) (Diamond 1975).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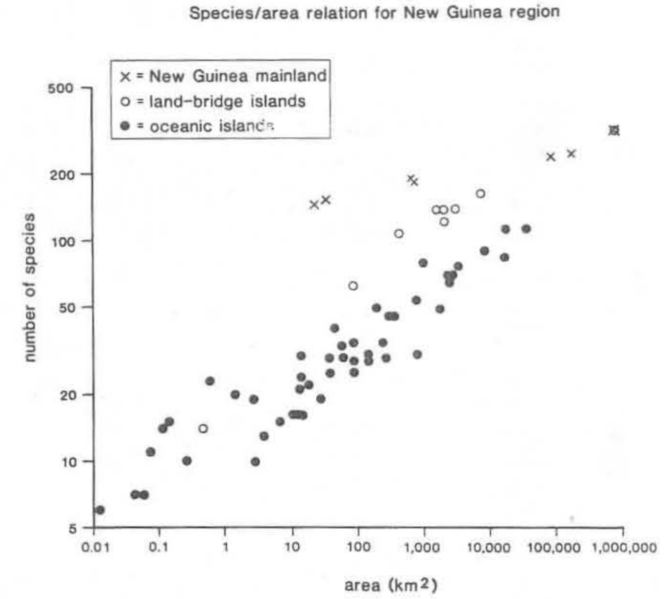

FIGURE 14. Species/area relation for bird species on oceanic islands (●) and land-bridge islands (o) of the New Guinea region, and for areas of various sizes on the New Guinea mainland (x). Note that land-bridge islands have fewer species than equivalent-sized areas of the New Guinea mainland, as a result of extinctions since the end of the Pleistocene period. Oceanic islands have fewer species than equivalent-sized land-bridge islands, except that very small land-bridge islands do not differ in species number from oceanic islands because of very high post-Pleistocene extinction rates.

Thus, small population size (small size of island or low population density of the species) is again the best predictor of proneness to extinction. Population variability appears important in a few cases.

3. Other studies. Studies of differential extinction of birds on land-bridge islands, based on analysis of total species number, are those of Terborgh (1974, 1975) for neotropical islands, Diamond (1975) for the Bismarck island of New Hanover, and Terborgh and Winter (1980) for five large islands off four continents. Studies based on non-water-crossing species alone are those of MacArthur, Diamond, and Karr (1972)

for Panamanian islands, and of Diamond and Gilpin (1983) for greater Sunda islands. All of these studies concluded that extinction rates are higher on smaller islands.

EXTINCTIONS OF LIZARD POPULATIONS ON LAND-BRIDGE ISLANDS FRAGMENTED AT THE END OF THE PLEISTOCENE

Post-Pleistocene extinctions of lizards on land-bridge islands in the Gulf of California have been studied by Soule and Sloan (1966), Case (1975), and Wilcox (1978, 1980, 1983). These analyses yielded the following conclusions:

1. Species losses decreased with island area, just as in the studies of birds and mammals on land-bridge islands (fig. 15).

2. The Gulf islands differ in time since the land bridge was severed, from 6,000 to 12,000 years. Wilcox (1978) was able to show, after partialling out variation in S due to area and latitude, that S decreases with time since severing of the land bridge: i.e., that extinction increases with time (fig. 16). This conclusion is to be expected, but there is no other set of Pleistocene land-bridge islands where it has been tested.

3. As usual, some species fared much better than others (Case 1975). Where abundances have been measured directly, abundant lizards such as Uta stansburiana and Cnemidophorus tigris are on many more islands than are rare lizards. Alternatively, if one correlates persistence with habits without considering abundance, one finds that species on few islands tend to be habitat specialists (e.g., Coleonyx variegatus, Streptosaurus m[illegible]lis, Phrynosoma coronatum) or else species at high trophic levels (the lizard-eating lizards Crotophytus wislizenii and C. collaris).

4. If one compares calculated extinction rates for lizards on the Gulf islands with those for birds on neotropical

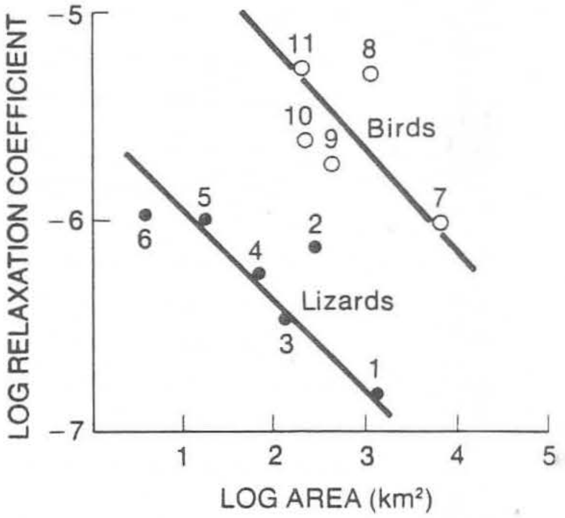

FIGURE 15. Risk of extinction (log relaxation coefficient: ordinate), as a function of island area (abscissa), for birds and lizards, on a time scale of 10,000 years. Extinction rates since the end of the Pleistocene were calculated for species on land-bridge islands of the New World. Note that risk of extinction decreases with area for both birds and lizards, but that bird populations go extinct over 10 times faster than lizard populations on an island of the same area (Wilcox 1980).

islands or mammals on western North American mountain tops, the values for lizards are an order of magnitude lower (Case 1975, Wilcox 1980; see fig.15). In fact, for birds on Gulf islands there is no difference between oceanic and land-bridge islands: all the Pleistocene populations of the land-bridge islands have disappeared, and the present avifauna consists entirely of subsequent overwater colonists (Wilcox 1983, Cody 1983). Thus, lizards are much less extinction-prone than birds and mammals on the same islands or on islands of similar area. The reasons are that lizards have much lower metabolic rates, tend to have higher population densities, and are far better able to survive

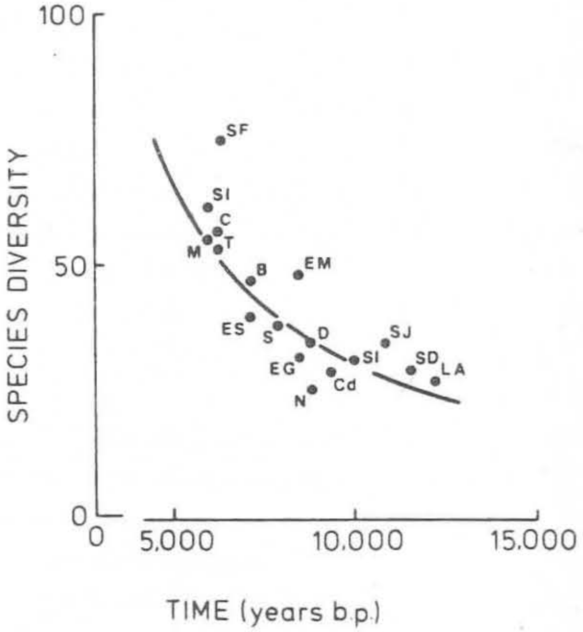

FIGURE 16. Calculated losses of lizard species on land-bridge islands near Baja California as a function of number of years elapsed since rising sea level severed the land bridge between each island and the Baja California mainland. The ordinate gives the number of lizard species corrected for variation due to area and latitude. Note that species number decreases with time because extinctions proceed with time. From Wilcox (1978): see Wilcox for identification of islands by letter.

long periods without food than are similar-sized birds and mammals (Wilcox 1978, 1980).

SUMMARY OF MAMMAL, BIRD, AND LIZARD STUDIES ON LAND-BRIDGE ISLANDS

Studies of extinction following late-Pleistocene fragmentation raise the same two methodological issues as did studies of extinction following modern fragmentation: assessing the initial biota, and separating the relative contributions of recolonization, and of resistance to extinction, in explaining modern presence.

Ideally, one would like to have the initial biota documented by fossils. The familiar difficulties in sampling the fossil record will generally frustrate this ideal. Among post-Pleistocene fragmentation studies to date, only the mammal studies have been able to draw on fossil evidence. In the absence of fossil evidence the initial biota must be inferred on the basis of the biota of similar-sized mainland areas today. Naturally, the mainland biota itself will have changed somewhat in the 10,000 years since the end of the Pleistocene. However, for the three studies involving mammals and with availability of fossils, it turns out that the fossils do not significantly alter any of the conclusions that would have been drawn if fossils had been unavailable.

Comparison of modern distributions and inferred late-Pleistocene ones yields unequivocal conclusions about extinction only if recolonization has been negligible. In the studies of mammals this assumption appears to be justified. The assumption would not be justified for an entire avifauna or herpetofauna. However, by confining attention to species unable to cross water gaps (as inferred from field observations and from absence from islands lacking Pleistocene land bridges), one can isolate sets of bird and lizard species that yield as unequivocal conclusions about extinction as do mammals. The analyses of Gulf of California lizards need reexamination from this point of view. The analysis of bird distributions on land-bridge islands by Terborgh and Winter (1980) encompassed all breeding land bird species, not just the non-water-crossers. This may explain why that analysis did not find clear relations between presence on land-bridge islands and expected correlates of resistance to extinction.

All studies of mammal, bird, and lizard extinctions on land-bridge islands have shown that populations on small islands are at greater risk than those on large islands.

Resistance to extinction correlated with direct estimates of abundance in three studies (Solomon birds, New Guinea birds, Gulf of California lizards), and with correlates of abundance (herbivory, small body size, generalized use of habitat) in four studies (Tasmanian, Sundan, and North American mammals and Gulf of California lizards). A few New Guinea bird species illustrated the expected dependence of extinction on population variability. Other expected correlates of extinction have not been tested in these studies of land-bridge islands.

EXTINCTIONS IN EVOLUTIONARY TIME, AS ESTIMATED FROM ENDEMISM

Some oceanic islands, such as Hawaii, Galapagos, and New Zealand, are famous for the endemism of their biotas, which consist mostly of endemic species and even genera and families. Other islands, such as the New Hebrides, Bismarcks, and Palau, lack such fame and share most of their species with the neighboring mainland or archipelago. What can be learned from these differences in endemism?

One can show that the number of species on an archipelago (or island) depends both on immigration rates and extinction rates, but that the percentage of an archipelago's species that are endemic to the archipelago depends only on extinction rates. That percentage, for some natural group of species such as birds, varies inversely with the average extinction rate for the group's species in the archipelago. The reason is that if populations go quickly extinct, few survive long enough to evolve into an endemic species or genus. Let the colonist pool outside the archipelago consist of P species with the probability p per unit time of colonizing the archipelago; and let q be the probability per unit time that a species present in the archipelago will go extinct. Then the number of species in the archipelago at any instant is $Pp/(p + q)$, a function of both the immigration probability p and the extinction probability q.

However, the fraction of the archipelago's species that survive for time t (e.g., for the time necessary to evolve into a distinct species) is simply e^{-qt}, a function only of the extinction probability q. The comparisons of archipelagoes (or islands) with respect to their percentages of endemics permits one to compare the risk of extinction among the archipelagoes.

At least five caveats require mention. First, the calculation obviously must exclude islands recently risen from the sea (e.g., Krakatoa and Surtsey), whose biota has had no time to differentiate and is entirely non-endemic for reasons unrelated to extinction. Second, one must similarly exclude islands recently covered by glaciers (e.g., Iceland); the biota of such islands is also necessarily recent. Third, one must exclude all Pleistocene land-bridge islands, on which endemism is very low because the island was a piece of the mainland so recently. A fourth point is that immigration does influence endemism insofar as gene flow from the mainland inhibits subspeciation and development of reproductive isolation. However, once reproductive isolation has been achieved, subsequent differentiation beyond the level of endemic allospecies (to the level of endemic full species, genus, or family) is not directly affected by immigrants. (Immigration rates may, however, have an indirect effect, by raising equilibrium species number and hence extinction rates.) Finally, while subfossil endemic bird species exterminated by the first Polynesian colonists are known for New Zealand and Hawaii, similar extinct subfossil endemics probably await discovery on other remote islands (Olson and James 1982). When subfossil avifaunas are better explored, consideration of them is expected to strengthen rather than change the conclusion drawn from fig. 17. Fig. 17 shows that the highest percentage of presently-known endemics is on large remote archipelagoes. It is precisely these archipelagoes, with their absence of native

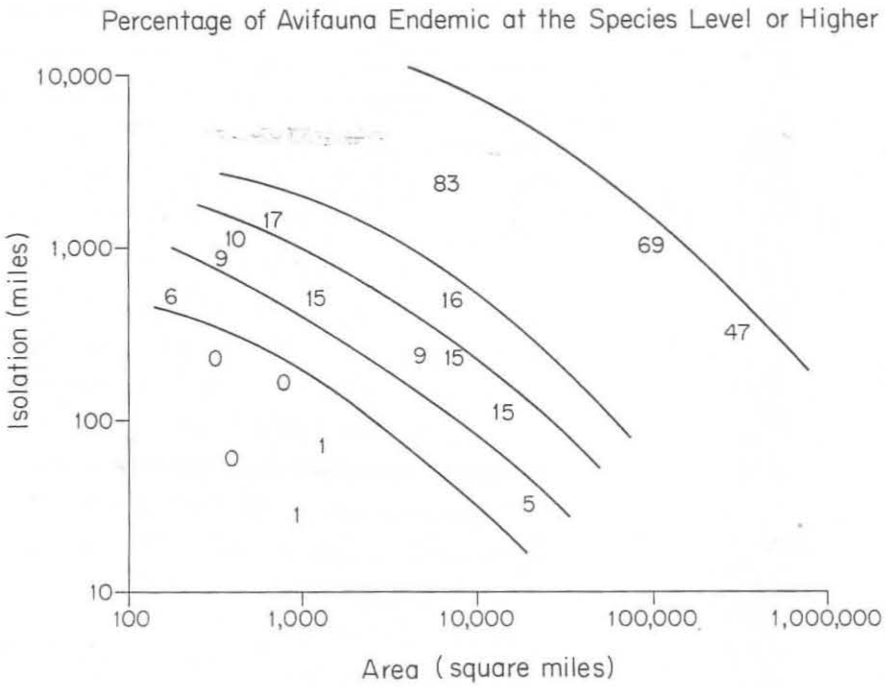

FIGURE 17. Numbers on the graph give, for some Pacific island or archipelago, the percentage of its breeding land bird species that are endemic at the level of full species or higher. Location of number gives the island´s area (square miles, abscissa) and distance from nearest major colonization source (miles, ordinate). For instance, 16% of the species of Fiji, with an area of 7055 square miles and distance of 520 miles from the New Hebrides, are endemic full species or belong to endemic genera. Curves are drawn by hand to group islands with similar endemism.. Note that endemism increases with island area and isolation. Since percentage of endemics is an inverse measure of the risk of extinctions, this means that extinction rates over evolutionary time are lowest on the largest, most remote islands (Diamond 1980).

mammals, that are most likely to have radiations of endemic birds that suffered extinctions when man arrived with his cats, rats, and pigs.

Fig. 17 shows how the percentage of endemic birds increases with archipelago area and isolation for Pacific island avifaunas (Diamond 1980). The Pacific islands with a high percentage of endemics are the huge, somewhat isolated islands of New Zealand (69%, including extinct subfossils), Australia (49%), and New Guinea (47%),and the medium-sized, very remote Hawaiian archipelago (83%; even higher when extinct subfossils are included). There is only a modest percentage of endemics on the large but close Solomons (15%) and Bismarcks (5), and on the remote but small Societies (17%) and Marquesas (9%). The reason why endemism increases with area is that extinction rates decrease with area over geological time, just as over shorter times (figs. 3, 4, 6, 9, 10, 12, 14, 15). Endemism increases with isolation because more remote archipelagoes receive fewer immigrants, hence fewer species at equilibrium, less competition, and lower extinction rates.

There are also differences in degree of endemism of various bird groups on the same island. For instance, of New Guinea's hawks, most (65%) belong to extralimital species, and only 10% belong to endemic genera, while the majority of New Guinea songbirds belong to endemic species and even genera. These differences become even more marked when one compares birds with other groups. For instance, Australia has numerous Gondwanaland relicts among its insects and plants, but almost all its endemic songbirds are products of a radiation from a post-Gondwanan colonization (Sibley and Ahlquist 1984). New Caledonia is a geologically old island on which volcanism ceased about 80 million years ago. It has endemic tribes of beetles and families of plants. Probable Gondwanan relicts include its mayflies and many beetles, and its podocarps, araucarias, Nothofagus, and Proteaceae among its plants (Holloway 1979). In contrast, among its 71 breeding land bird species only one (the kagu Rhinochetus jubatus) is even conceivably a Gondwanan relict, while 66 are not generically distinct, 52 are not specifically distinct, and 26 are not even subspecifically distinct.

These comparisons suggest that birds are much more extinction-prone than beetles, which have lower metabolic rates and higher population densities, and than many plant groups with longer lifetimes and higher population densities. The hawk-vs.-songbird comparison for New Guinea suggests higher extinction rates for hawks due to their lower population densities. However, it is risky to assess extinction proneness of different groups on the same island by means of differences in levels of endemism alone without fossil evidence. The very low endemism of New Guinea hawks may be due to high immigration rates preventing achievement of reproductive isolation. The same factor may explain why endemism is so much lower in Hawaiian ferns than Hawaiian insects. Molecular evidence from protein and DNA clocks makes it obvious that taxa of the same nominal level of endemism in different groups can be of very different ages, e.g., species of frogs or rodents considered congeneric on morphological grounds are far more distinct than congeneric bird species (Wilson _et_ _al_. 1977; Sibley and Ahlquist 1982). In short, since we do not know whether songbirds can differentiate to the level of being considered an endemic genus more rapidly than can hawks or ferns and less rapidly than can beetles, the intergroup comparisons of endemism are equivocal indicators of proneness to extinction. This objection does not apply to comparison of the same group in different archipelagoes.

CONCLUSIONS

I began with six theoretical predictions about population lifetimes (resistance to extinction): that they would increase with generation time or individual lifetime, population density, area, intrinsic rate of increase, and ratio of birth to death rate, and that they would decrease with variability in population size. The data base for testing these conclusions comes from studies of turnover in communities at equilibrium, modern habitat fragmentation, late-Pleistocene land or habitat fragmentation, and endemism. How well do the predictions stand up?

All studies confirm that risk of extinction decreases with area available to the population. (The increase in habitat diversity as well as population size with area surely contributes to this decrease in the risk of extinction.)

Studies of turnover, modern fragmentation, and late-Pleistocene fragmentation confirm that risk of extinction decreases with population density, either measured directly or else inferred from its correlates of trophic position, body size, and habitat niche width.

The prediction concerning variability in population size is confirmed by turnover studies, and supported by fragmentary data from the Barro Colorado fragmentation study and the New Guinea land-bridge island study.

The prediction concerning individual lifetime is confirmed by turnover studies.

The predictions concerning intrinsic rate of increase and ratio of birth to death rate have not been tested.

I suggest two steps for carrying these analyses of extinction further:

First, if one compares populations of different species on the same island, the effect of population density on risk of extinction is so steep (fig. 2) that it will be impossible to discern effects of other factors until the effect of this overriding factor has been removed. Indirect correlates of population density (trophic position, body size, and habitat niche width) will not suffice for this purpose. The first step should therefore be direct measurement of population density and construction of an e-vs.-N graph like fig. 2.

Second, one may then try to interpret species with deviantly high or low values on e-vs.-N graphs in terms of the species' lifetime or generation time, population variability, intrinsic rate of increase, and birth and death rates. Some of this life-history information can already be culled from the literature. Thus, I have hopes that we can make progress soon in understanding how species differ in susceptibility to extinction, in terms of biological attributes of the species.

It is a pleasure to acknowledge my debt to Lee Jones, Egbert Leigh, Jr., Robert May, Timothy Reed, the late Gordon Williams, and S. Joseph Wright for valuable information and discussion.

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